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Field colonization, population growth, and dispersal of *Boreioglycaspis melaleucae* Moore, a biological control agent of the invasive tree *Melaleuca quinquenervia* (Cav.) Blake

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Abstract

Invasion of native plant communities by the Australian paperbark tree (“melaleuca”), *Melaleuca quinquenervia*, complicates restoration of the Florida Everglades. Biological control, within the context of a comprehensive management program, offers a means to suppress regeneration of melaleuca after removal of existing trees and a mechanism to forestall reinvasion. To meet this need, a biological control program commenced in 1997 upon the release of an Australian weevil (*Oxyops vitiosa* [Pascoe] [Coleoptera: Curculionidae]). Release of a second biological control agent, the melaleuca psyllid (*Boreioglycaspis melaleucae* Moore), followed in February 2002 at field sites containing mixed age-class melaleuca stands or coppicing stumps. Each site was inoculated with 7000–10,000 adult psyllids, with one exception where 2000 nymphs were released on seedlings the following December. Psyllid populations established everywhere irrespective of colony source, site conditions, or the quantity released, although numbers released and, to a lesser degree, colony age influenced the numbers of colonies produced. Quantity included in the release was the major determinant of the resultant number of colonies, although the duration of their tenure in quarantine culture may have also influenced this. One site, comprised mainly of coppicing stumps, contained 3.3 million psyllids per ha within 3 months after release. Less than 1% of the coppices at a similar site harbored psyllid colonies 2 months after release (May 2002), but this rose to 75% in October then to 100% by December. The census population exceeded 715,000 adults and nearly 11 million nymphs by late January 2003. Psyllid populations dispersed 2.2–10.0 km/year, with the slower rates in dense, continuous melaleuca stands and faster rates in fragmented stands. Over 1 million psyllids had been redistributed to 100 locations as of December 2005. This species now occurs throughout much of the range of melaleuca in south Florida due to natural range expansion as well as anthropogenic dissemination.
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1. Introduction

Melaleuca quinquenervia (Cav.) S.T. Blake (Myrtaceae), the five-veined paperbark tree (hereafter “melaleuca”), is a large (25–30 m tall), native Australian tree. It naturally occurs in wetlands along the eastern coast of Queensland and New South Wales (11–34 °S) (Boland et al., 1987). It rapidly naturalized in Florida after being imported during the late 19th century as an ornamental landscape plant (Dray, 2003). Development threatens melaleuca habitat in Australia (Turner et al., 1998), but it is a prolific wetland invader in Florida, especially in the fire-maintained ecosystems that typify the southern portion of the peninsula (Laroche and Ferriter, 1992).

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Southern Florida largely consists of a unique system of marshes, rivers, sloughs, and tree islands collectively known as the ''Florida Everglades''. These fragile ecosystems provide water resources vital to the sustenance of both urban and agricultural lands as well as to natural areas. The Florida Everglades have steadily degraded over the past century as drainage and anthropogenic diversion of the original sheet flow altered hydrological regimes (Ogden, 2005). Paradoxically, while similar activities have despoiled melaleuca habitat in Australia, they have probably favored this species in Florida (Hofstetter, 1991). A major effort is now underway to modify the hydrology of southern Florida so as to restore some semblance of the structure and function of the original wetland systems (Ogden, 2005). This restoration effort, which focuses upon managing water, may be thwarted by the encroachment of nonindigenous plants, particularly melaleuca, into native communities (Ferriter et al., 2005). Recovery of these systems will therefore require management of adventive species as well as rejuvenation of historic water flow patterns (Davis and Ogden, 1994).

Control of melaleuca is complicated by the massive, canopy-held seed bank, which stores as many as 25 billion seeds per hectare (Rayamajhi, unpublished data). These seeds are released en masse when fire, felling, or herbicide applications disrupt vascular connections thereby causing the capsules to desiccate and open. Even though a low proportion of the seeds are viable (Rayamajhi et al., 2002), seedling densities of 10 million individuals per hectare are not uncommon following such events (Center, unpublished data). Sustainable management of melaleuca therefore depends on removing existing stands while simultaneously preempting regeneration and preventing reinvasion. Hence, a biological control program was developed that emphasizes curtailing seed production and reducing recruitment from seedlings and saplings. The leaf-feeding melaleuca snout beetle, *Oxyops vitiosa*, released during 1997, has partially fulfilled this goal (Center et al., 2000; Pratt et al., 2005) but, because it pupates in the soil, it does not thrive in inundated habitats. A second biological control agent, the melaleuca psyllid, *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), completes its life cycle entirely on the plant (Purcell et al., 1997; Wineriter et al., 2003) and is less vulnerable to hydrological conditions. It should therefore establish viable populations even where *O. vitiosa* cannot.

The small adult psyllids (3–4 mm) as well as the nymphs are free-living phloem-feeders. Adult females oviposit directly on the surface of leaves or stems. Each egg bears a pedicel that the female inserts into the plant tissue, which may function in water absorption as it does in other species (White, 1968). Like most psyllids, *B. melaleucae* development advances through five nymphal instars and requires 28–41 days (Purcell et al., 1997) but this varies depending upon temperature and host quality (Hodkinson, 1974). First instar nymphs are active after eclosion but soon settle in a fixed position to begin feeding and tend not to move unless disturbed (Wineriter, personal observation). The 3rd to 5th instars secrete a white, waxy flocculence (Wineriter et al., 2003) which often covers an aggregation of several individuals, including earlier instars. This flocculence is thought to impede desiccation (Hodkinson, 1974) and its occurrence signals the presence of this otherwise inconspicuous insect. However, the abundance of flocculence is diminished by heavy rains. Smaller instars often reside within the partially opened stem tips between the expanding leaves. Both adults and nymphs feed presumably by inserting their mouthparts into stomata and resulting feeding damage has been associated with the injection of phytotoxic salivary exudates (Hodkinson, 1974; Purcell et al., 1997; Morath et al., in press). Adults hop or make short flights when disturbed, often flying vertically and then spiraling down to land near their original location. The release, field colonization, population growth, and dispersal of this important biological control agent are presented herein.

2. Materials and methods

2.1. Source of insects and pathogen screening

Psyllids released in Florida descended from parental stock collected at Brisbane, Queensland, Australia, and nearby locales (all within 100 km of one another) during April 1997 until November 2001 (Table 1) and then maintained in a quarantine containment facility over varying durations. All colonies were reared on live plants in a similar manner using methods described by Wineriter et al. (2003). A single plant enclosed with a screen cage was inoculated with approximately 25 females and 10 males and reared for a single generation. A similar number of F_1 adults from the several hundred produced were then removed to inoculate a new cage. This procedure was necessary to limit the numbers in the cages and prevent the overpopulation and host deterioration that would inevitably result, so it was performed continuously during the tenure of this insect in quarantine.

New psyllid colonies held in quarantine were checked for pathogens by S.E. White (Microbiologist, USDA-ARS, CMAVE, Gainesville, Florida) every 3–4 months by sacrificing a portion of the adult population. Samples of adults from all six colonies were again examined on February 7, 2002, 6 days prior to the first release. Psyllids were aspirated into vials either one day prior to or on the day of examination. The longer holding period was intended to stress the adult psyllids to facilitate the detection of latent disease organisms. Groups of either 50 or 100 adults were homogenized in distilled water. Samples of the crude suspensions were then examined with phase-contrast illumination using a compound microscope.

2.2. Verification of identifications

Adult psyllids were aspirated from the quarantine colonies into 55.5 ml (15-dram) vials. They were examined

Table 1
Derivation of *Boreioglycaspis melaleucae* adults released from the Florida Biological Control Laboratory FDACS quarantine facility, Gainesville, by the USDA-ARS Invasive Plant Research Laboratory

Colony No.	Date received in Quarantine	Collection locality (Queensland, Australia)	Nos. used to initiate colony		
			Eggs	Nymphs	Adults
1	3 May 1997	Indooroopilly, Logan	0	1–30	11
	7 Jun 1997	Indooroopilly, Logan	0	<30	3–4
	1 Jul 1997	Indooroopilly	0	≈20	0
2	4 Oct 1997	Bracken Ridge	0	<75	5
3	15 May 1998	Indooroopilly	0	<32	2 ♂:12 ♀
4	13 Jan 1999	Indooroopilly	0	<119	0
5	13 Nov 2001	Tewantin, Silverwood Dr.	0	0	2 ♀
	3 Dec 2001	Tewantin, Silverwood Dr.	100s	0	35 ♂: 46 ♀
6	13 Nov 2001	Landsborough, Ewan Maddock Dam	0	0	3 ♂:4 ♀
	3 Dec 2001	Landsborough, Ewan Maddock Dam	100s	0	5 ♂:10 ♀

either on the day they were collected or on the following day (held overnight at 5 °C). Douglass R. Miller (US National Museum of Natural History, Washington, DC), Susan E. Halbert (Florida Department of Agriculture and Consumer Services, Gainesville, FL), and Gary R. Buckingham (USDA-ARS, Gainesville, FL) confirmed identities of individuals in the first group released from quarantine; Buckingham and Halbert confirmed later releases. Psyllids were removed from quarantine into adjacent facilities in preparation for release.

2.3. Field colonization

After identification, psyllids were placed directly onto caged 1-m tall melaleuca plants that had been grown in 3.8-L (1-gal.) pots. The plants were enclosed within "no-see-um" mesh (246 holes/cm^2) sleeve cages, similar in size and construction to those described by Wineriter et al. (2003). Each cage was inoculated with 300–400 psyllids then transported to either the Invasive Plant Research Laboratory (IPRL, USDA, ARS) at Fort Lauderdale, Broward Co., Florida, or directly to field sites. A total of 45,965 psyllids were thus transferred during the period of 12 February to 18 April 2002.

Adult psyllids were initially released at five melaleuca-invaded sites (Table 2): Andytown (Broward Co.), Picayune Strand (Collier Co.), Pennsuco Wetlands (Dade Co.), Estero (Lee Co.), and Arthur R. Marshall National Wildlife Refuge (NWR) (Palm Beach Co.). A later ceremonial public release was made at Everglades Holiday Park (Broward Co.). A portion was also released in research plots at IPRL and used as stock for later releases. Field sites were inoculated by placing pots containing the psyllid-infested plants on the ground, removing the screens, and intermingling the foliage with that of the local melaleuca trees. In some cases, pots were placed in plastic bags that were partially filled with water. The bags were tightly wrapped around the base of the plant. This reduced drought stress and provided ample time for the psyllid nymphs to mature and disperse. Nymphs were released on seedlings at a seventh site (Loxahatchee Slough) in Palm Beach County the following December. Populations were considered established if they persisted at the release sites for at least one year.

2.4. Site descriptions

Release sites (Table 2) represented most of the major melaleuca-dominated habitats present in south Florida. The Andytown site consisted of clumps of melaleuca stems sprouting from stumps that had been cut near ground level (coppices). The soil at this site was sometimes saturated, but rarely flooded. The Picayune Strand State Forest flooded during the summer rainy season. Melaleuca had consequently become the predominant tree after several fires (latest June 1998) killed most of the native pines. The stands were characterized by scattered mature, reproductive trees ($\geqslant$15 m) surrounded by dense populations of saplings ranging in height from 0.5 to 5 m. The Pennsuco wetlands was a 5261 ha natural area where adverse hydrologic changes and disturbances had converted the original sawgrass marshes and spikerush sloughs to large monocultures of melaleuca. The melaleuca population was dominated by large, reproductively mature trees ($\geqslant$15 m) with scattered juveniles along the periphery. The Estero site, once a pine flatwoods that had been invaded by melaleuca, had been ditched for drainage to provide pasturage. Most of the melaleuca trees had been cut at ground level, which left thousands of scattered stumps. These consistently coppiced after being mowed two to three times a year, producing young foliage year round. Large trees (5–15 m) remained where mowing was untenable. The southern portion rarely flooded but the lower northern portion occasionally flooded during severe rainfall events. The Arthur R. Marshall Loxahatchee NWR site consisted of an isolated melaleuca head on a bog island. Trees at the center were large (≈10 m) whereas those at the periphery and outlying individuals varied from medium (≈3 m) to large. The Everglades Holiday Park site was in the same degraded marsh as the Andytown site and it rarely flooded. It consisted of an isolated melaleuca head with trees that varied from large ($\geqslant$15 m) in the main stand to small,

Table 2
Locations of initial releases, numbers and stages of psyllids released, and results

Site	Release date	Coordinates (DD)		Psyllids		Plant type	*Oxyops vitiosa* presence	Established
		°N	°W	Number	Stages			
1. Andytown	13 Feb 02	26.03585	−80.4347	8000	Adults	Coppices	Yes	Yes
2. Picayune Strand	14 Mar 02	26.10429	−81.6358	8000	Adults	Saplings	Yes	Yes
3. Pennsuco Wetlands	14 Mar 02	25.81130	−80.4173	7000	Adults	Large trees	No	Yes
4. Estero	18 Mar 02	26.42537	−81.8088	8000	Adults	Coppices	Yes	Yes
5. Holiday Park	9 May 02	26.06020	−80.4424	10,000	Adults	Large and medium	Yes	Yes
6. IPRL Lab	9 May 02	26.08447	−80.2379	5000	Adults	Saplings	Yes	Yes
7. Loxahatchee Slough	6 Dec 02	26.81536	−80.2053	2000	Nymphs	Seedlings	No	Yes
8a. Loxahatchee NWR	21 Mar 02	26.59240	−80.36046	10,180	Adults	Medium to large	No	No
8b. Loxahatchee NWR	9 July 02	26.59240	−80.36046	1400 and 400	Nymphs and adults	Pollards	No	Yes

dense saplings (1–2 m) at the stand margins and scattered further out into the adjacent sawgrass. The psyllids were placed mainly on the smaller peripheral trees by participants at this ceremonial public release. The Loxahatchee Slough Natural Area was comprised of cypress swamps, marshes, and wet prairies, interspersed with pine flatwoods and hammocks. Northern portions of this fragmented wetland system had been invaded by melaleuca. The release site consisted of a solitary melaleuca stand that had burned several years earlier, resulting in high seedling densities (503–2256 seedlings/m^2).

2.5. Colony age vs. size of release as determinants for establishment

We compared the ability of the various colonies to establish at the Andytown site to determine if prolonged tenures in quarantine, which possibly induced inbreeding depression, affected field colonization. We chose to use a single site so as to avoid the variation due to habitat differences. A 5×5 m grid had previously been established at the site wherein each grid intersection was demarcated with a labeled stake. Twenty-one psyllid-infested ''donor'' plants were placed at the site on 13 February 2002. Seven supported psyllids colonized for two to three generations (3–4 months) from recent importations (October and November 2001; denoted as ''new''); twelve others from colonies held in quarantine for 27–41 generations (4–5 yr, from 1997 to 1998; denoted as ''old''). Each donor plant was inoculated with psyllids from either a single new or old quarantine colony or a mixture from all old colonies or both new colonies. Numbers of psyllids from the various colonies were limited by availability. We nestled each plant within a randomly selected coppicing stump (''recipient plant'') while removing the cage to release the psyllids. The cages were removed carefully to avoid disturbing the adults so they would remain in place. The donor plants held an average of 394 (range 50–783) psyllid adults; averaging 247 females (range 36–458) and 168 males (range 10–168). The ''old'' donor plants held an average of 382 (range 82–726) individuals; averaging 205 (range 50–469) females and 177 (38–429) males. The ''new'' donor plants harbored an average of 414 (range 50–783) individuals; averaging 247 (range 36–458) females and 168 (range 10–385) males. The potted donor plants were left in place to allow the psyllids to transfer to the adjacent plants as the donor foliage desiccated.

This approach succeeded because the adult psyllids tended to remain at the point of release as described earlier. They are short-lived so the populations perpetuated mainly from the nymphs that hatched from eggs deposited on the donor plants or on foliage of the recipient plant. The nymphs were able to crawl to the intermingled foliage of the recipient plants as the potted donor plants deteriorated. The release foci thus remained discrete with minimal dispersal to adjacent plants.

The completely randomized experimental design that was used included two treatments: old colonies and new colonies. The evaluation criterion was the number of colonies produced on the recipient plants. The location of each donor plant was based on the random selection of a numbered grid intersection point. Both sexes were present on most donor plants (numbers had been counted upon removal from quarantine) but, in addition to the 19 plants described above, one was infested with only males (200) and one with only previously mated females (250). The donor plant with only males was intended as a check for dispersal within the site. The one with only females was intended to determine if it was necessary to include males in the release. Preliminary data from each recipient coppice included the relative abundance of the weevil *O. vitiosa* (absent, low, medium, or high) and the severity of weevil damage (1, minor; 2, substantial; 3, heavy).

The recipient coppices were evaluated on 29 March 2002. This 44-d period approximated the time required for completion of one generation (Purcell et al., 1997). The colonies, being composed mainly of nymphs during the intervening period, remained concentrated on the recipient plants so we were able to capture data before the psyllid had dispersed throughout the site. The numbers of psyllid colonies present on the old and young foliage of each recipient coppice were counted. The psyllids prefer to colonize young foliage, so we counted tips bearing new growth on each coppice as a measure of resource availability. The presence or absence of nymphs and adults was noted as were *O. vitiosa* eggs, larvae, or adults and spores

or symptoms of infection by a rust fungus (*Puccinia psidii* G. Wint.; see Rayachhetry et al., 2001). Damage by *O. vitiosa* or rust was rated on a 6-point scale based upon the proportion of foliage affected (0, no damage; 1, <25%; 2, 25–49%; 3, 50–74%; 4, ⩾75%; 5, no green foliage remaining). Psyllid damage was rated on a 5-point scale: 0, none; 1, flocculence only; 2, leaf discoloration; 3, leaf abscission; 4, branch dieback. Psyllid establishment on each recipient coppice was rated on a three-point scale: 1, not established, no psyllids found; 2, tenuous establishment, psyllids present but difficult to find; 3, well-established, psyllids easily found.

The average numbers of colonies produced from the "old" and "new" colonies was first compared using the nonparametric *G*-statistic. The colony of only males was excluded, leaving seven data points for the new colonies and 13 for the old. However, because the size of the releases were not consistent, we also analyzed the data using a general linear model to perform analysis of covariance (Proc GLM, SAS Institute, 1999) with colony age as the main effect, release size as the covariate, and an age by release size interaction using the following model:

$$\hat{Y} = a(\text{age}) + b(\text{size}) + c(\text{size} * \text{age}) + \varepsilon.$$

The interaction was not significant ($P = 0.8338$) so this term was excluded from the final analysis. This analysis controlled for variation attributable to the number of individuals released. Correlation analyses (Proc CORR, SAS Institute, 1999) were also done to determine if a relationship existed between the number of colonies produced and the number of females included in the release, the number of males included, the proportion of females, or the number of growing stem apices. The amount of new growth was also compared between old and new colonies using one-way analysis of variance (Proc GLM, SAS Institute, 1999). The effects of damage by *O. vitiosa* on colonization intensity was examined using analysis of covariance as above with the size of the release as the covariate.

2.6. Population growth and expansion

Censuses were conducted following releases at the Andytown and Estero sites. Population estimates were possible at these sites because the short stature of the coppices permitted inspection of all of the foliage, whereas this was not achievable where larger trees predominated. Only one census was done at Andytown on 3 January 2003 (324 days post-release). Censuses had been ongoing at Estero since October 1998 at approximately 6-week intervals to estimate *O. vitiosa* population density (Center et al., 2000). Psyllids, which were released on 18 March 2002, were included in the counts beginning on 5 December 2002 (262 days post-release), but presence/absence data were collected as early as May. Subsequent sampling, which was done on 22 January, 7 March, and 23 April 2003, terminated when the site was disrupted for development. The point-quarter distance method, normally used in forestry to estimate tree density, also seemed appropriate for stumps, so the number of live coppices was estimated using this technique (Cottam and Curtis, 1956; Krebs, 1999). Sampling involved selecting a series of random points, in these cases by randomly selecting grid intersection points, then partitioning the area surrounding each point into quadrants (NE, SE, SW, and NW). Distance from the point to the center of the nearest live coppice in each quadrant was measured to the nearest centimeter. The 5×5 m grid at Andytown and a 20×20 m grid at Estero (see Center et al., 2000) were used to randomly select sampling points. Fifty points were sampled at Estero (200 coppices) and 20 points were sampled at Andytown (80 coppices) and tree density was determined from the formula

$$\hat{N}_p = 4(4n-1)/\pi \sum (r_{ij}^2) \quad \text{(Krebs,1999)},$$

where $\hat{N}_p$ is the estimate of population density, n is the number of random points, and r_{ij} is the distance (in meters) from point i to the nearest coppice in quadrant j. This provided an estimate of the coppice density (plants/m^2), which was multiplied by the site area to determine the total number of coppices within the delimited sector (8.09 ha at Estero, 0.50 ha at Andytown). Plant injury caused by psyllids was rated on a 6-point scale according to the proportion of the foliage affected (0, no damage; 1, <25%; 2, 25–49%; 3, 50–74%; 4, ⩾75%; 5, no green foliage remaining). The presence or absence of psyllid eggs was noted on each coppice and the number branch tips were tallied. The numbers of visible psyllid adults were also tallied while gently manipulating the foliage to avoid any undue disturbance that would induce them to fly.

All aboveground biomass was harvested from 25 randomly selected coppices. These samples were transported to laboratory facilities where 10% of the stems were subsampled to count nymphs. Leaves were individually removed and examined using a stereomicroscope. Numbers of nymphs were tallied according to their stage of development (early and late instars). The density per plant was then estimated by multiplying the number of nymphs per stem by the number of stems per plant. The total nymph and adult populations on site were determined by multiplying this product by estimates for the number of live coppices at the site.

Adults and discrete psyllid colonies (as indicated by discontinuities in the dispersion of nymphal flocculence) were tallied and the presence or absence of eggs was noted during the single sampling at the Andytown site. These counts encompassed all of the foliage on all four plants at each of the 20 sampling points. The nymphal density was estimated by multiplying the average counts from 19 randomly selected colonies by the average number of colonies per plant. Estimates per site were derived as described above.

2.7. Rate of spread and spatial distributional patterns

The rate at which *B. melaleucae* dispersed from the original release points was quantified at the Estero, Picayune Strand State Forest, and Pennsuco Wetland locations. In general, these incipient psyllid populations were separated

from other such populations by at least 60 km. Also, *M. quinquenervia* trees at these sites were widely, although sometimes patchily, distributed in all directions. The location of the release point was fixed at each site using real-time differential global positioning (GPS; Trimble Pathfinder Pro XR®: Trimble Navigation Limited, Sunnyvale, CA 94086). Data were collected in decimal degrees with resolution accuracy to the fourth decimal place. We allowed 5 min of averaging to occur for each GPS reading before recording the coordinates. Data were imported into the geo-referenced software ArcView GIS version 3.2a (Environmental Systems Research Institute, Inc., Redlands, CA), and graphical output was in the Mercator projection type.

Flocculence produced by immature psyllid stages is diagnostic (Wineriter et al., 2003) and discloses the presence of the otherwise cryptic colonies, even at very low population densities. Melaleuca trees were searched for this evidence of psyllid presence along transects radiating outward from the release point in the four cardinal directions (N, S, E, and W; Caughley, 1970). Searches extended from the epicenter to a minimum of 0.75 km beyond the last observed indication of psyllid presence in order to locate the most distant occurrence on each transect. This point was flagged with colored plastic surveyor's tape so as to demarcate a starting point for later surveys. Dispersion from each release point was quantified monthly beginning 27–30 days after psyllid release until February 2003 at Miami and Estero and until October 2002 at Picayune Strand State Forest. Plant density was estimated at the latter site in six 1-m^2 plots placed at intervals along each transect with two additional plots near the release point ($n = 26$). The number of various *M. quinquenervia* life stages was tallied in each plot.

We calculated the rate of spread for each site from psyllid dispersion along each transect as

$$R = \frac{\left[(d_N^2 + d_S^2 + d_E^2 + d_W^2)/4\right]^{1/2}}{t},$$

where R is the rate of spread (km/year) for an individual site, d is the distance (km) traveled by *B. melaleucae*, N, S, E, and W represent transects in the 4 cardinal directions, and t is time (years) after release (adapted from Andow et al., 1993).

Various characteristics of each transect were noted to elucidate parameters that might have influenced the rate of spread. These included direction, stand fragmentation, hydroperiod, predominant wind direction, and maximum and mean wind speed. Melaleuca fragmentation along each transect was categorized into 3 levels: low—dense continuous stands with breaks <30 m, moderate—isolated stands separated by breaks of 31–200 m, and high—widely dispersed patches separated by more than 200 m. Hydroperiod was classified in accordance with Ewel (1990): dry—never inundated; short—inundated <6 months; moderate—inundated 6–9 months. Wind data from 2002 to 2003 were used which were gathered at 1-h intervals from individual weather monitoring stations located <40 km from each study site. Wind direction was categorized into 8 components (N, NE, E, SE, S, SW, W, NW). Stepwise regression identified parameters that influenced the linear distance traveled by *B. melaleucae* along each transect. The criteria for including or excluding an explanatory variable was $P < 0.05$ and $\geqslant 0.05$, respectively (SPSS, 1999). Analysis of variance (ANOVA), followed by Tukey HSD, was used to compare the effects of categorical parameters on dispersal distances.

3. Results

3.1. Source of insects and pathogen screening

Six laboratory colonies established in quarantine from 10 importations (Table 1). The first four provided for experiments designed to delineate and predict the host range of this insect (Wineriter et al., 2003); the last two colonies were established after completion of host-range studies in preparation for forthcoming releases. No pathogenic organisms were ever detected using the screening methods employed at CMAVE (Wineriter et al., 2003). The subsequent report concluded that "no spores, sporangia, or occluded viruses were found ... no evidence that unoccluded viruses or excessive bacteria were present ... the colonies appeared free from pathogens."

3.2. Verification of identifications

Each examiner scrutinized the contents of each vial and confirmed the identity of every psyllid focusing on visible diagnostic characters, such as the pronounced genal processes (Burckhardt, 1991). No other psyllid species were found. A few vials that contained contaminants (small flies, collembolans, etc.) or immature psyllids were rejected. The majority were authorized for release. Voucher specimens were lodged at the Florida State Collection of Arthropods. Specimens had previously been sent to various other repositories (Wineriter et al., 2003).

3.3. Field colonization

Boreioglycaspis melaleucae colonies established readily regardless of the quantity or stage released, the demographic structure of the melaleuca stand, the presence or absence of *O. vitiosa*, or the hydrology of the site (Table 2 and Fig. 1). The largest release of 10,000 adults at Holiday Park produced the weakest establishment, but this was attributable to uncontrollable circumstances during the public event. Abnormally high mortality of the psyllids occurred due to delays, heat, and excessive or inexpert handling during the public event. The smallest release of 2000 nymphs onto seedlings at the Loxahatchee Slough site was also successful, despite the handling involved in transferring young nymphs. Furthermore, establishment was attained on individual

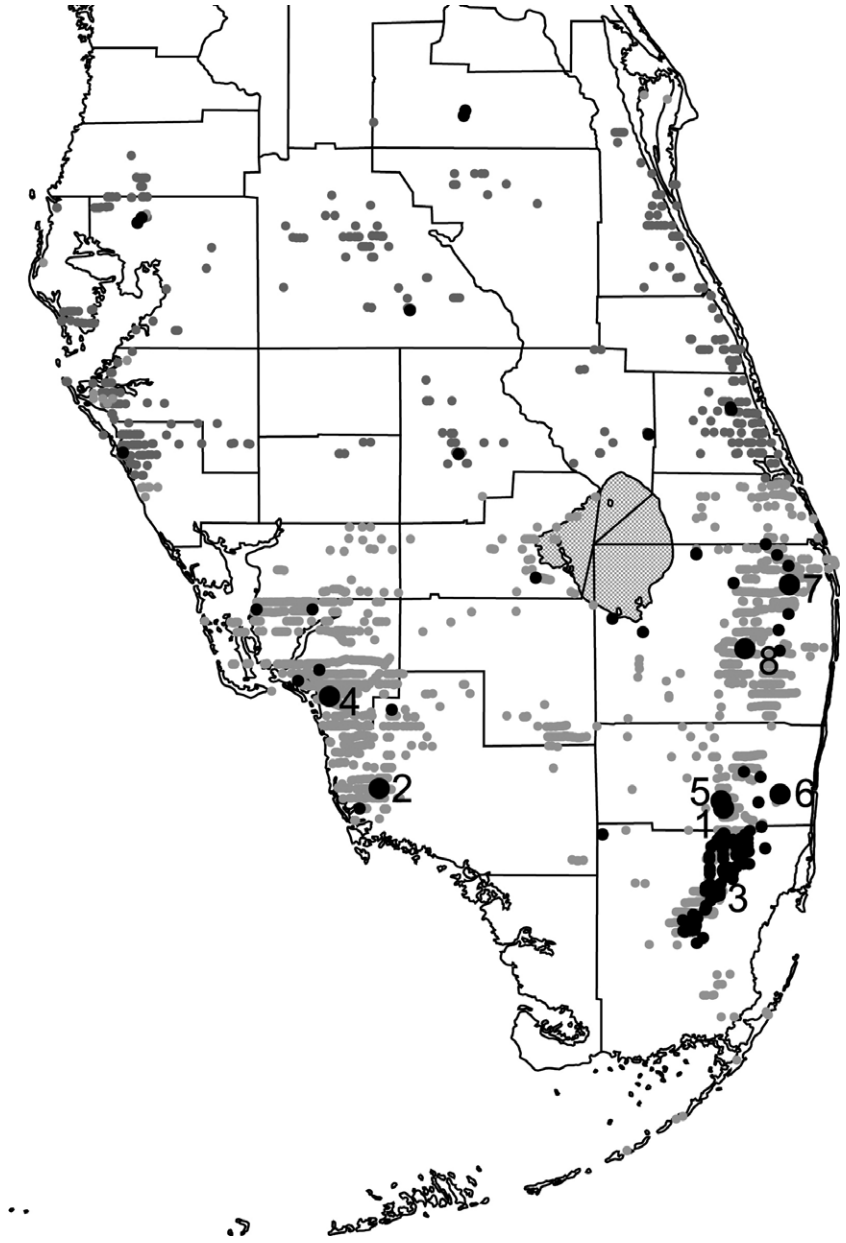

Fig. 1. A map of southern Florida showing original release sites (large dots) along with redistribution locations (smaller dots). The site numbers match those in Table 2 and the gray dots represent the distribution of melaleuca.

coppices at the Andytown site with as few as 50 adults. Thus, it seemed that the number of individuals released was inconsequential in terms of whether or not establishment was achieved. Colonies established abundantly on the luxuriant new growth of pollards (i.e., stumps of trees cut well above ground level) or coppicing stumps (Estero, Andytown, and Loxahatchee NWR) but they also readily colonized seedlings (Loxahatchee slough), saplings (Picayune), and mature trees (Holiday Park). Colonies developed at the permanently inundated Loxahatchee NWR site as well as at seasonally wet (most sites) and dry locales (Estero and IPRL garden plots).

Psyllid colonies established after a single release at most sites, but two attempts and some site preparation were necessary at Loxahatchee NWR. The first release during March 2002 involved planting 12 psyllid-infested *M. quinquenervia* saplings in the marsh at the edge of the stand. We detected nymphs on 10 of the 12 original 'donor' plants during the next visit on 26 June 2002, but nothing on the local trees. None of the local trees were flushing new growth so refuge personnel cut them at breast height on 9 July 2002 to induce the dormant buds to produce new foliage. Abundant new growth was present on the pollards by October 8, 2002, but no psyllids were detected. We therefore released an additional 1400 nymphs and 400 adults. Psyllid nymphs were easily found during the next visit (January 18, 2003) on the regrowth foliage. We released another 1500 adults that we had carried to the site,

but they were probably not needed. Numerous colonies were present when the site was last examined on July 8, 2003.

3.4. Colony age vs. size of release as determinants for establishment

Psyllids rapidly transferred from the donor plants to 20 of the 21 recipient plants placed at the Andytown site. Not surprisingly, the plant originally infested with only males represented the single exception and illustrated the lack of dispersal within the site. Densities ranged from 2 to 305 colonies/coppice ($\overline{X} = 73.0$, SE = 18.7) when the releases were evaluated. These colonies still remained concentrated at points of release. Nymphs resided on all 20 coppices but adults were present on only half of them: five of the 13 coppices (38%) inoculated from "old" colonies and five of the seven (71%) inoculated with "new" stock. This intermittent presence of adults indicated the recent emergence of F_1 generation adults so the evaluations had been done at an appropriate time before they had begun to disperse.

Higher average colony densities developed on the seven plants inoculated with psyllids from "new" stock ($\overline{X} = 114.1$ colonies/coppice, SE = 40.4, range 14–305) as compared to the 13 plants that received "old" stock ($\overline{X} = 50.9$ colonies/coppice, SE = 16.7, range 2–234). A comparison of these values using the nonparametric *G*-statistic indicated that the difference was significant ($G_{adj} = 12.6$, $P < 0.001$).

We were concerned that this result might have been influenced by the size of the releases so the effect of colony age on establishment success was reanalyzed using analysis of covariance (SAS Institute, 1999) with the number of individuals in each release included as the covariate. The model explained a significant amount of the variation in the number of new colonies (square root transformed) produced ($R^2 = 0.57$, $F = 11.4$, $P = 0.0007$). In this analysis, the age of the colony seemed to affect the number of colonies produced (Type I SS, $F = 5.81$, $P = 0.03$) when the size of the release was not considered. However, when variability attributable to the size of the release was removed, the role of colony age diminished (Type III SS, $F = 4.01$, $P = 0.06$). The number of individuals released was the primary factor determining the number of colonies produced ($F = 17.0$, $P = 0.0007$) but colony age also mattered, although to a lesser extent (Fig. 2). When the data were adjusted for the number of individuals released, an average (least square mean) of 86 colonies were produced from new stock as compared to 41 from old stock ($P = 0.06$). Releasing more females produced more colonies (Pearson's correlation $r = 0.67$, $P = 0.001$) but the number of males was immaterial ($r = 0.39$, $P = 0.09$), as was the proportion of females ($r = 0.01$, $P = 0.96$). Colonies established even on the one recipient plant that had been inoculated with only females; although the resultant colony density was low (250 females produced only three colonies).

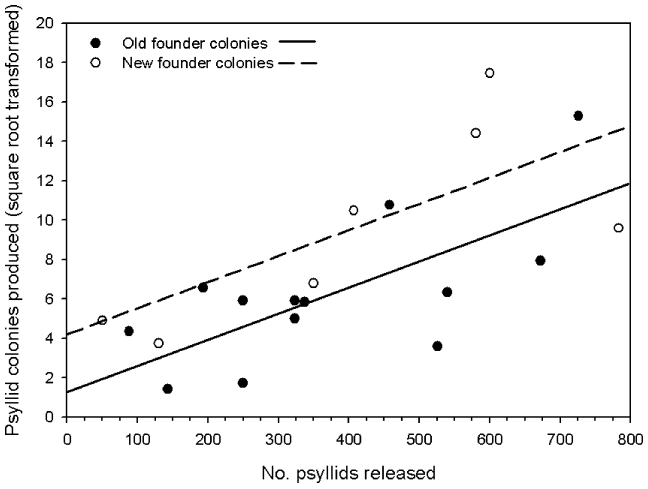

Fig. 2. Results of the analysis of covariance comparing the effects of the age of the founder colonies and the numbers of psyllids released on the level of establishment in terms of the quantity of new colonies produced.

All recipient coppices exhibited new growth when we released the psyllids, but the amount of new foliage available varied considerably. Nonetheless, the number of colonies present on each coppice was independent of the availability of young foliage as exemplified by expanding stem apices (Pearson's correlation $r = 0.01$, $P = 0.96$). The amount of new growth was essentially the same on plants infested with new vs. old colonies ($\overline{X}_{new} = 165$ vs. $\overline{X}_{old} = 169$ tips per coppice; $F = 0.21$, $P = 0.65$). The relationship between colony age and establishment success consequently did not change after taking resource availability into account.

We had considered that the presence of the weevil *O. vitiosa* or the associated amount of plant damage might have influenced establishment of the psyllids, but there was too little initial variation in levels of weevil damage within the site to support comparisons. The initial weevil density was rated as "absent" or "low" on 80% of the coppices, and "medium" to "high" on only 20% of the coppices. Likewise, damage was low on 12, medium on six, and high on only two of the recipient coppices at the time of release. Differences became more apparent at the conclusion of the study, however, when damage was rated "low" on seven, "medium" on eight, and "high on five of the coppices. Interestingly, psyllid colonization increased along with increasing weevil damage wherein averages of 29, 72, and 138 colonies were present on coppices exhibiting the three respective levels of weevil damage (Fig. 3). Analysis of covariance indicated that the number of colonies produced was, in fact, correlated with weevil damage, even after adjusting for differences in the number of females released (square root transformed data, Type III SS, $F = 4.06$, $P = 0.04$). This association was positive, however, so the weevils clearly did not interfere with the psyllid's ability to establish and this probably related to psyllid-induced defoliation causing the plants to produce new foliage which attracted the weevils.

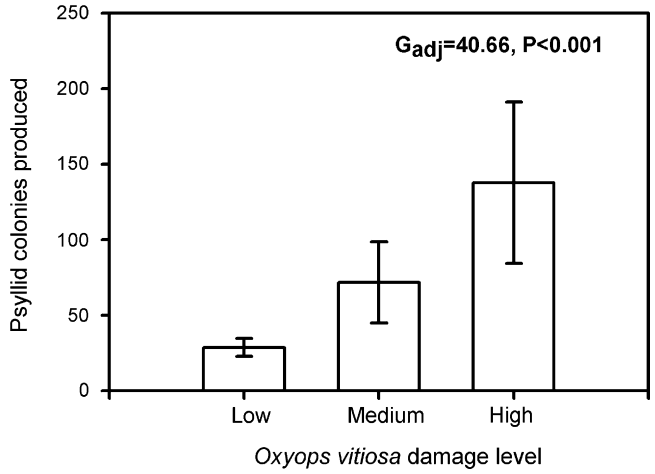

Fig. 3. The relationship between the amount of weevil damage on the recipient plants and the level of establishment by the psyllids.

Rust infection on the recipient plants was consistently low with ratings of 0 or 1 on 19 of the 21 coppices, and ratings of 2 on the remaining two coppices. The presence of the rust fungus was therefore not a factor in the establishment of the psyllids.

3.5. Population growth and expansion

We estimated that 870 coppicing melaleuca stumps existed at the Andytown site within the 0.5 ha study area. The census conducted on 3 January 2003, 324 days after the release revealed that psyllids were on all but one of the 80 plants examined (i.e., 99%), and eggs were observed on 54%. The psyllid population was estimated at 1336 nymphs per plant based on averages of 47 (±6.7) nymphs per colony and 29 (±3.5) colonies per plant. Each plant also harbored an average of 5.2 (±0.9) adults. The population was thus estimated to have grown at least 139-fold to 1.17 million adults and nymphs from the original 8393 adults. This represented an underestimate because a portion of the *B. melaleucae* population had dispersed into surrounding areas where they could not be censused. Nonetheless, this conservative estimate represented a daily increment based on exponential growth of 1.53% and a 46-day doubling time.

We first observed psyllids within the pasture at the Estero site during May 2002, about 2 months after they had been released along the adjacent ditch, but they had infested a mere 0.5% of the coppices. Infestation rates increased during July and August to 15% and 11%, respectively, then to 75% by October and 100% by December, when the population was estimated at over 193,000 adults and 2.2 million nymphs. Numbers peaked in January 2003 at 715,581 adults and 10.9 million nymphs. The psyllid population had declined to an estimated 324,943 adults and 4.7 million nymphs by April, mainly due to a lack of live foliage. At this time, psyllid feeding had caused most of the coppicing shoots to drop their leaves and the remainder had taken on a brown and burnt visage from the desiccating foliage.

A nearly identical pasture existed east of the ditch where the psyllids had been released. The psyllid dispersed in both directions so that both sides were equally infested. We did not census the somewhat larger eastern pasture; it was assumed that at least as many psyllids were present there as in the western section. Hence, the original 8000 psyllids released on 18 March 2002 produced a peak population 310 days later of at least 23 million individuals. This represented a 2900-fold increase in less than a year, a daily increment of 2.60%, and an average population doubling time of 27 days, assuming exponential growth. Again, these are underestimates inasmuch as they do not account for emigration.

3.6. Rate of spread and spatial distributional patterns

When averaged among all directions and sites, *B. melaleucae* spread from release points at a rate of 4.71 (±0.37) km/year. The predictive equation for psyllid dispersal through the melaleuca-dominated habitat over time was best described as:

$$y = 5.85 + (0.532 * s) + (0.008 * t) + (-5.370 * r) + (-0.339 * w) + (-0.018 * p),$$

where y is the distance (km) dispersed, s represents the site, t is the time after release, r is relative humidity, w is wind direction, and p is the total precipitation measured at monthly intervals ($R^2 = 0.44$). Psyllid dispersal varied by site ($df_{2,112}$; $F = 5.71$; $P = 0.0044$), with a higher rate of spread at the Estero site (10.22 ± 2.71 km/year) as compared to the Miami (2.05 ± 0.25 km/year) and Picayune Strand State Forest (1.83 ± 0.09 km/year) locations (Fig. 4). Psyllid dispersal accelerated from the release points over time ($df = 1$; $t = 7.25$; $P < 0.0001$), ranging at the Estero site from an initial 9.2–3745 m/month one year after introduction. Average rate of spread for all sites was

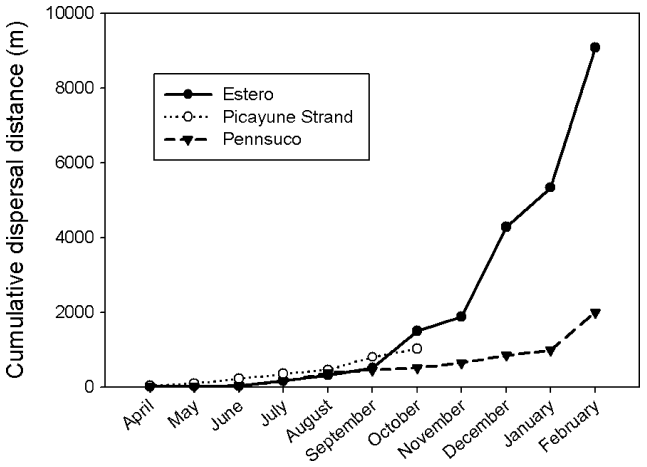

Fig. 4. Cumulative distance dispersed by *B. melaleucae* following release at three south Florida locations.

225.0 (±76.1) m/month. Dispersal distance decreased with increasing levels of both relative humidity and precipitation ($df = 1$; $t = 2.08$; $P < 0.0400$; $df = 1$; $t = 1.65$; $P < 0.102$, respectively). Wind directions were primarily from the SE (79%) and S (14%), resulting in greater dispersal distances along northern transects ($df_{3,112}$; $F = 4.93$; $P = 0.003$).

4. Discussion

An introduced biological control agent can be viewed as a new invader and as such offers the opportunity to learn more about the invasion process. A biological invasion involves four discrete stages: arrival, establishment, dispersal, and range expansion (Memmott et al., 2005). Attention has been given to the quantity of individuals (i.e., propagule size) involved in an invasion (Memmott et al., 2005), but quality may be equally important. Indeed, as Crawley (1986) notes, a main determinant in establishment (i.e., invasion success) is the invader's intrinsic rate of increase. This may relate to the "quality" of invaders in terms of reproductive capacity, and in turn, to the vitality of the propagules. This has long been a concern among biological control practitioners inasmuch as an agent species may be reared in an insectary for prolonged periods before being released which can lead to inbreeding depression, founder effects, genetic drift, and selection of laboratory-adapted strains (Mackauer, 1976, 1981).

Our small study which compared the short-term establishment success of "old" vs. "new" colonies showed that field colonies established from all source material but those from recently imported stock increased in size more quickly. The increased benefit of releasing more individuals was the same for both the old and new stock (i.e., slopes of the regression trajectories were equal) but more than twice as many colonies resulted from the release of new stock when counts were adjusted for the number of individuals released (i.e., adjusted means differed). This suggests that the duration of insectary colonization did not affect the *rate* of establishment but retention of stock over prolonged periods may have adversely affected the *level* of establishment. The effect of colony age was marginal, however, inasmuch as this accounted for only about 10% of the total variation in the number of colonies produced after release size was taken into account. This validates the rearing methods used which preserved the viability of the original stock over 4–5 years and as many as 41 generations. The most important factor, though, was clearly the number of individuals released inasmuch as more females produced better establishment. This suggests that the somewhat lowered quality of the source colonies caused by prolonged rearing could be compensated for or offset entirely by simply releasing more individuals.

Boreioglycaspis melaleucae now occurs across a wide range of habitats in Florida, being less restricted by hydroperiod than *O. vitiosa*. Psyllid populations established quickly and readily at all release sites irrespective of the age of the colony, site conditions, or the quantity released. Although the psyllids were thought to be less fastidious than *O. vitiosa* in terms of their choice of host tissue, they preferentially colonized flushes of young foliage, the presence of which facilitated establishment (as shown by the site preparation at Loxahatchee NWR). Coppicing stumps produce rapidly growing shoots (Kruger and Reich, 1993a,b) which provide an abundant resource to support psyllid population growth. As a result, numbers increased exponentially where coppices predominated and psyllids quickly spread to infest virtually every melaleuca plant within the sites. The Andytown site, for example, produced 3.3 million psyllids per ha within 3 months after releasing 8000 individuals. All of the coppices at the 8.1-ha Estero site harbored psyllid colonies within 9 months (December 2002) and the census population exceeded 715,000 adults and nearly 11 million nymphs after 10 months (late January 2003). This bodes well for this agent if, as Crawley (1986) asserts, that species with high realized rates of population growth are more likely to suppress weed populations.

Thus far, there has been little evidence that parasites, predators, or diseases regulate the psyllid populations although this has yet to be closely examined. We have observed generalist predators, primarily coccinellids, syrphid larvae, chrysopids, and spiders, predating psyllid nymphs, and adults but with seemingly little impact. There was also no evidence that the previously introduced weevil *O. vitiosa* interfered with the ability of the psyllid to establish. The fact that the level of establishment increased along with increasing weevil damage suggests that one facilitated the other or perhaps that both preferred similar types of plants. Periods of heavy precipitation seemed to suppress the psyllid populations but they quickly rebounded during dry periods so the flocculence may have simply washed away causing the colonies to be less conspicuous. In-depth studies on biotic and abiotic mortality factors are needed to better understand these dynamics.

Psyllid populations dispersed quickly at rates ranging up to 10.0 km/year. This contradicts Crawley's (1986) analysis wherein he noted that insect biological control agents tended to spread more slowly on long-lived plant species and more rapidly on short-lived herbaceous species. Compared to other weed biological control agents released in Florida, *B. melaleucae* dispersed much more rapidly than *O. vitiosa* which ranged from 0.10 to 2.8 km/year (Pratt et al., 2003) but more slowly than the waterhyacinth moth (*Niphograpta albiguttalis* (Warren)) which dispersed nearly the length of the state (over 500 km) in about 18 months (Center, 1984). Like *O. vitiosa*, but in contrast to *N. albiguttalis*, *B. melaleucae* populations persisted and continued to increase at release sites despite active dispersal to other areas. *O. vitiosa* and *B. melaleucae* are effective biological control agents whereas *N. albiguttalis* is not (Julien and Griffiths, 1998; Franks et al., 2006; Morath et al., in press; Pratt et al., 2004, 2005; pers. obs.). This suggests that vagility and rapid dispersal may not necessarily be desirable traits; whereas philopatry leading to

"aggregated attack" (Zwölfer, 1985) may be advantageous. Even in programs with rapidly dispersing agents, however, redistribution efforts are often implemented to expedite herbivore spread and impacts on target weeds. In response to observed impacts of the psyllid, federal, state, and county agencies initiated a redistribution campaign for *B. melaleucae* in 2003. Approximately 1 million psyllids had been redistributed to nearly 100 locations (Fig. 1) as of December 2005. Studies to examine the realized geographic distribution of *B. melaleucae* as a result of this release effort and the landscape-level heterogeneity of herbivore impacts are underway.

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